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Genetic Relationships of Crown Rust Resistance, Grain Yield, Test Weight, and Seed Weight in Oat

J. B. Holland
United States Department of Agriculture

Gary P. Munkvold
Iowa State University, munkvold@iastate.edu

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J. B. Holland* and G. P. Munkvold

ABSTRACT

Integrating selection for agronomic performance and quantitative resistance to crown rust, caused by *Puccinia coronata* Corda var. *avenae* W.P. Fraser & Ledingham, in oat (*Avena sativa* L.) requires an understanding of their genetic relationships. This study was conducted to investigate the genetic relationships of crown rust resistance, grain yield, test weight, and seed weight under both inoculated and fungicide-treated conditions. A Design II mating was performed between 10 oat lines with putative partial resistance to crown rust and nine lines with superior grain yield and grain quality potential. Progenies from this mating were evaluated in both crown rust-inoculated and fungicide-treated plots in four Iowa environments to estimate genetic effects and phenotypic correlations between crown rust resistance and grain yield, seed weight, and test weight under either infection or fungicide-treated conditions. Lines from a random-mated population derived from the same parents were evaluated in three Iowa environments to estimate heritabilities of, and genetic correlations between, these traits. Resistance to crown rust, as measured by area under the disease progress curve (AUDPC), was highly heritable (H = 0.89 on an entry-mean basis), and was favorably correlated with grain yield, seed weight, and test weight measured in crown rust-inoculated plots. AUDPC was unfavorably correlated or uncorrelated with grain yield, test weight, and seed weight measured in fungicide-treated plots. To improve simultaneously crown rust resistance, grain yield, and seed weight under both lower and higher levels of crown rust infection, an optimum selection index can be developed with the genetic parameters estimated in this study.

Crown rust, one of the most widespread and damaging diseases of oat (Harder and Haber, 1992), can reduce grain yields (Endo and Boewe, 1958; Frey et al., 1973) and grain quality traits such as seed weight and groat percentage (Simons and Browning, 1961; Simons et al., 1979). Host plant resistance is the most economical control measure of oat crown rust (Harder and Haber, 1992).

The most common form of resistance exploited by oat breeders to date completely prevents reproduction of the fungus on the host and segregates as a single gene. Monogenic resistance historically has not remained effective in North America longer than 5 yr after the resistance genes were released in pure-line cultivars (Holland, 1997). Monogenic resistances can be overcome rapidly by new races of the pathogen that emerge because of the selection pressure exerted by large areas of uniformly resistant hosts (Harder and Haber, 1992; Kolmer, 1997). Evolution of new races in crown rust populations can occur via accumulation of mutations in asexual populations or by sexual recombination on the alternate host, buckthorn (*Rhamnus cathartica* L.), which occurs naturally in North America (Chong and Kolmer, 1993; Dinoor et al., 1988).

Methods proposed to improve the durability of crown rust resistance in oat include gene pyramiding, gene deployment, multiline breeding, and selection for partial resistance. Gene deployment, wherein breeders in different regions agree to release cultivars with different sets of resistance genes, should exert disruptive, rather than directional, selection pressure on the pathogen population (Frey et al., 1973). Multilines are expected to exert stabilizing, rather than directional, selection on the pathogen (Frey, 1982). Both gene deployment and multiline breeding strategies depend upon the availability of large numbers of effective resistance genes, which are not currently available for crown rust resistance in oat. Compared with resistance from a single major gene, gene pyramiding may enhance the durability of resistance because it should be more difficult for virulence to two or more major resistance genes to develop in a single fungal genotype. The combination of resistance genes *Pc38* and *Pc39* was released in the Canadian cultivars Dumont, Riel, and Robert, and in the North Dakota cultivars Steele and Valley (McMullen and Patterson, 1992). This combination of genes was no more durable than typical single gene resistances. Simultaneous virulence to both *Pc38* and *Pc39* became frequent in Canadian rust populations after the release of cultivars with this gene combination (Chong and Kolmer, 1993).

Partial resistance should be more durable than race-specific, complete resistance because selection pressure on the rust population is reduced (Simons, 1972). Evolution of virulence to partial resistance is expected to be slower than to complete resistance, although *Puccinia recondita* Roberge ex Desmaz populations responded to

J.B. Holland, USDA-ARS, Plant Science Research Unit, Dep. of Crop Science, North Carolina State Univ., Box 7620, Raleigh, NC 27695-7620; G.P. Munkvold, Dep. of Plant Pathology, Iowa State Univ., Ames, IA 50011. Journal Paper No. J-18658 of the Iowa Agric. and Home Economics Exp. Stn., Ames, IA, Project No. 3368 and 3260. Received 1 Sept. 2000. *Corresponding author (james_holland@ncsu.edu).

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Abbreviations: AUDPC, area under the disease progress curve; SCA, specific combining ability.

artificial selection for a shorter latent period on partially resistant wheat hosts, suggesting that fungal populations can evolve to overcome quantitative partial resistance (Shaner et al., 1997). Durability of resistance is impossible to prove except in retrospect, but Stuthman (1995) noted that the oat cultivar Portage has maintained its high level of partial resistance to crown rust from the time of its release in 1960 to the present.

Two major impediments to selection for partial resistance to rust diseases are the difficulty in measuring partial resistance accurately and the generally quantitative inheritance of partial resistance. Area under the disease progress curve (AUDPC), which is based on measurements of the percentage of leaf area infected made periodically during the growing season, is a useful measure of partial disease resistance in the field, but is very labor-intensive to measure. Partial resistance can also be characterized by its components, including latent period, infection efficiency, infectious period, and spore production (Brake and Irwin, 1992; Parlevliet, 1979). Partial resistance is usually polygenically inherited and often has low heritability, although there are exceptions to this (Brake and Irwin, 1992; Parlevliet, 1979; Simons, 1972).

Simons (1972) suggested that measurement of tolerance traits is a more reliable method to identify genotypes with partial resistance than is direct measurement of partial resistance. Simons (1966) estimated tolerances for grain yield and seed weight of many oat genotypes grown in hill plots as ratios of the traits measured in plots inoculated with *P. coronata* to the traits measured in rust-free plots in the same experiment. Heritabilities of yield and kernel weight tolerance ratios were large enough to allow progress from selection for tolerance in either trait (Simons, 1969); however, tolerance was, in some instances, associated negatively with yield potential (Simons, 1985). Rosielle and Hamblin (1981) suggested that tolerance to stress will generally be correlated negatively with yield potential, and that selection for tolerance is often not an appropriate breeding strategy. Carson and Wicks (1989) suggested that selection for yield under disease stress is expected to result in increased disease resistance and grain yield potential in the absence of disease stress. Selection for grain yield under northern leaf blight [caused by *Exserohilum turcicum* (Pass.) Leonard and Suggs] and diplodia stalk rot [caused by *Stenocarpella maydis* [Berk.] Sutton] disease stress in a maize population resulted in significant increases in grain yield in the absence of disease stress and in disease resistance, but did not significantly improve grain yield under disease stress (Carson and Wicks, 1993).

Oat cultivars that produce high grain yields with good grain quality under both crown rust-free environments and crown rust-conducive environments are ideal for North Central U.S. production environments, where the disease is endemic, but varies in intensity from year to year. We suggest that an appropriate strategy to develop such cultivars with potentially more durable resistance to crown rust is to evaluate genotypes under both inoculated and rust-free conditions and to consider grain yield, test weight, and seed weight under inoculated conditions and grain yield, test weight, and seed weight under rust-free conditions as separate traits that can be included along with disease severity in a selection index.

The objectives of this study were to (i) develop an oat population segregating for quantitative genes affecting grain yield, test weight, and seed weight, and resistance to crown rust; (ii) test for both additive and nonadditive genetic effects on resistance to crown rust, measured as AUDPC; and (iii) estimate heritabilities and genotypic and phenotypic correlations of crown rust severity, grain yield, seed weight, and test weight measured in crown rust-infected plots; grain yield, seed weight, and test weight measured in plots without substantial crown rust infection; and grain yield, seed weight, and test weight tolerance ratios. The results of this experiment will guide future efforts to develop durably resistant oat cultivars with good agronomic performance.

MATERIALS AND METHODS

Inoculum

Race nonspecific partial resistance can be indistinguishable from race-specific complete resistances controlled by separate genes if a heterogeneous pathogen population is used as the inoculum (Parlevliet, 1992). In such a situation, a race-specific gene with major effects on resistance would prevent infection by a part of the inoculum population, resulting in a disease reaction that may appear to be partial resistance. Therefore, we used a single isolate of *P. coronata*, isolate 345, from the Iowa State University *P. coronata* collection as inoculum for all experiments. This isolate is compatible with many *A. sativa* hosts (Wise and Gobelman-Werner, 1993).

Urediniospores stored in evacuated glass tubes in liquid N were heat-shocked at 40°C for 10 min and increased in the greenhouse by inoculating plants of the susceptible oat cultivar, Markton. Urediniospores were collected by aspiration from greenhouse plants and used immediately for field experiments or desiccated and stored at −80°C in microfuge tubes. For field inoculations, urediniospore suspensions (approximately 10^5 mL^{-1}) were prepared in sterile distilled water with 0.20% (v/v) Tween 20.

Population Development

Ten cultivars and lines were selected on the basis of previous field evaluations to serve as donors of putative partial resistance genes ("rust resistance donor parents," Table 1, Fig. 1). MN841810 and MN841823 are experimental lines developed at the University of Minnesota that have exhibited durable partial resistance to crown rust. UQP4-1 and UQAsc-1 are experimental lines developed at the University of Queensland, Australia. UQP4-1 is a selection from the cross of 'Panfive', which has good partial resistance to crown rust (Brake and Irwin, 1992), and 'Panfour'. UQAsc-1 is a selection from the cross of Panfive and 'Ascencao'. H632-518 was reported previously to have good seed weight tolerance to crown rust (Simons et al., 1987). Ten cultivars and lines with excellent grain yield and agronomic performance but lacking complete resistance to predominant races of crown rust in Iowa were also selected to serve as donors of favorable alleles for grain yield and other agronomic traits ("yield donor parents," Table 1, Fig. 1).

The 10 resistance donor parent lines were mated to the 10 yield donor parent lines using a Design II mating scheme

Table 1. Means of yield donor and rust resistance donor parent oat lines and cultivars and Markton check for crown rust AUDPC and agronomic traits measured under crown rust inoculation and in plots treated with a systemic fungicide to limit crown rust infection, estimated from four environments in 1997 and 1998.

	Traits measured in crown rust-inoculated plots				Traits measured in fungicide-treated plots			Means over rust treatments	
Line	AUDPC	Grain yield	100-seed weight	Test weight	Grain yield	100-seed weight	Test weight	Heading date	Height
		g m^{-2}	g	kg m^{-3}	g m^{-2}	g	kg m^{-3}	dap†	m
Yield donor parents									
Armor	205	159	1.97	319	281	2.65	405	65	0.98
Brawn	33	258	2.93	371	315	3.17	398	68	0.94
Don	58	227	2.45	406	241	2.55	416	63	0.90
Hazel	28	216	2.61	392	280	2.73	413	66	0.97
IAR30-20	57	199	2.49	363	244	2.63	379	63	0.98
Ogle	137	215	2.48	336	290	2.94	405	65	0.99
Prairie	53	275	2.52	372	333	2.78	394	66	0.98
Premier	199	151	2.18	346	255	2.57	453	66	0.96
Sheldon	193	162	2.28	340	271	2.70	414	62	1.03
Starter	181	151	2.52	342	234	2.83	407	63	0.96
Group mean	115	201	2.44	359	274	2.75	409	65	0.97
Rust resistance donor parents									
Calibre	51	215	2.44	370	271	3.14	415	71	1.06
H632-518	102	122	2.57	401	158	2.67	402	62	1.05
Jim	30	264	2.67	421	334	2.91	424	63	1.02
Milton	30	229	2.44	376	314	2.76	429	68	0.95
MN841810	47	200	2.72	385	254	2.96	418	67	0.99
MN841823	97	148	2.64	304	228	2.93	333	67	1.08
Moore	102	188	2.28	375	278	2.81	419	67	1.07
UQP4-1	122	117	2.22	321	164	2.33	372	61	0.93
UQAsc-1‡	140	113	2.06	–	133	2.20	–	63	0.96
Portage	29	140	2.58	369	206	2.66	408	68	1.18
Group mean	75	174	2.46	369	234	2.74	402	66	1.03
Resistance vs. yield Parents	***	***	NS	*	***	NS	NS	***	***
Markton‡	265	63	1.63	–	245	2.32	–	71	1.10
LSD 0.05	44	67	0.25	31	67	0.25	29	2	0.06

* $P = 0.05$.
*** Mean of rust resistance donor parents significantly different from mean of yield donor parents at the $P = 0.01$.
NS, no significant difference between mean of rust resistance donor parents and yield donor parents.
† Days after planting.
‡ UQAsc-1 and Markton did not produce sufficient grain to measure test weight.

(Hallauer and Miranda, 1988). F_2 and F_3 bulk progeny from each of these 100 matings were grown as entries in field evaluations of the Design II mating in 1997 and 1998. In addition, unrelated F_1's from the Design II mating were intermated to produce 83 full-sib families (4-way crosses) (Fig. 1). S_0 plants from each 4-way cross were grown as spaced plants in Aberdeen, ID, and S_1 seed was harvested separately from each S_0 plant. A single, randomly chosen S_1 plant from each of two randomly chosen S_0 plants per cross was grown in the greenhouse in autumn, 1997. S_2 seed was harvested separately from each S_1 plant. Ten randomly chosen S_2 progeny per S_1 plant were grown in the greenhouse in spring, 1998. S_3 seed descended from a common S_1 parent was harvested in bulk to form $S_{1:3}$ families. Four of the 4-way crosses produced only one S_0 plant, so a total of 162 $S_{1:3}$ families were developed in this way. We also developed 36 $F_{3:5}$ families from the biparental crosses using the greenhouse in the same way. These additional families were included to make the allelic contribution of each original parent to the population approximately equal. The $F_{3:5}$ and $S_{1:3}$ families together constituted 198 lines representing the random-mated population used to estimate heritabilities and genotypic and phenotypic variances and covariances. The expected amounts of inbreeding and heterogeneity within and between families are identical for $F_{3:5}$ and $S_{1:3}$ families, so we refer to all lines in the random-mated population as $S_{1:3}$ families.

Selection for polygenic partial rust resistance is predicted to be effective only in populations lacking major genes conferring complete resistance to the inoculated isolate (Cox, 1995). Therefore, we grew the 20 parental lines in the greenhouse and inoculated them as seedlings with *P. coronata* isolate 345 to test for the presence of major resistance genes in the parental lines. All parental lines, except the cultivar Jim, exhibited a fully susceptible seedling reaction. Jim was completely resistant to the isolate as a juvenile plant. The greenhouse screening was performed after the population development crosses were made, therefore, Jim and all of its progeny were included in field evaluations. These entries were included in some of the statistical analyses to provide information on complete and incomplete block effects, but they were eliminated from analyses designed to estimate correlations or heritabilities, or to test for additive and nonadditive genetic effects (Fig. 1).

Design II Mating Experiment

F_2 progenies from each of the 100 matings in the Design II crossing experiment, along with each of the parent lines plus the susceptible check cultivar, Markton, were included as entries in a field experiment grown in 1997 at the Iowa State University Agronomy and Agricultural Engineering Research Farm, Boone Co., IA. The experimental design was a split-plot with inoculation treatment [either inoculation with *P. coronata* or treatment with the systemic fungicide triadimefon, 1-(4-chlorophenoxy)-3,3-dimethyl-1-(*H*-1,2,3-triazol-1-yl)-2-butanone, to prevent crown rust disease] as the whole-plot factor and genotype as the sub-plot factor. The experiment was replicated twice, each replication of a treatment was designed as an 11 by 11 square lattice. Plots were hills of 30 seeds each planted on a grid and spaced 0.3 m in perpendicular

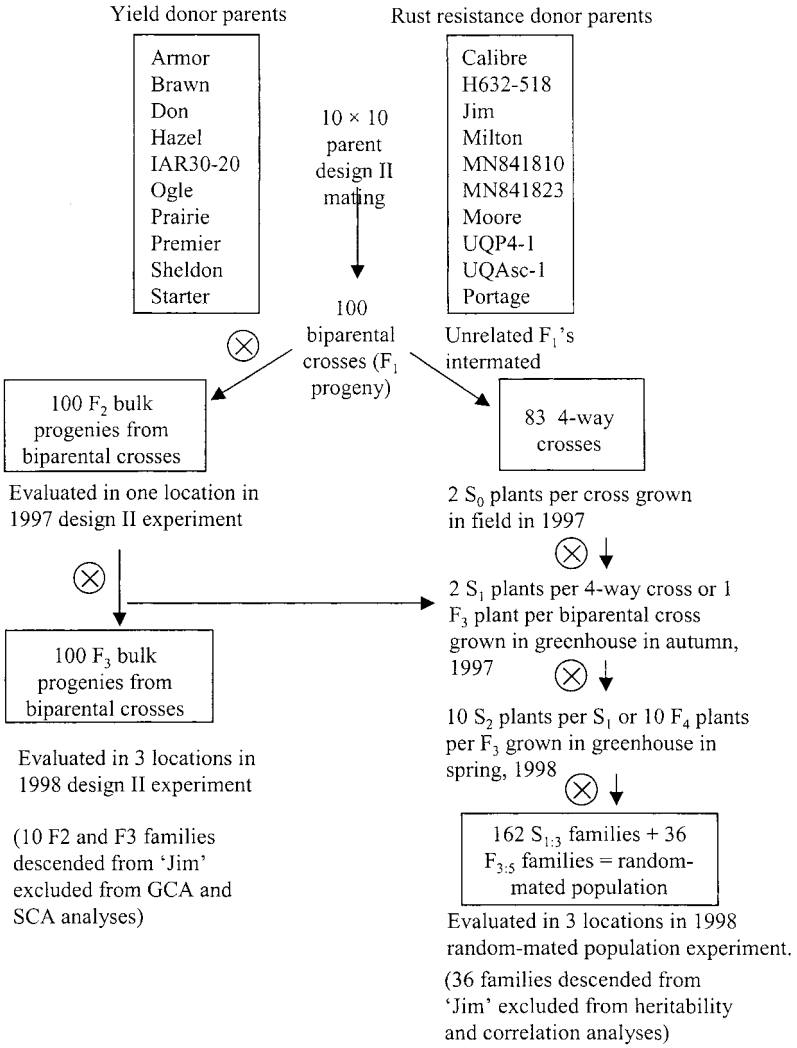

Fig. 1. Development of oat populations using a Design II mating of 10 "rust resistance donor" parents and 10 "yield donor" parents, followed by natural self-fertilization to produce F_2 and F_3 bulk progenies and $F_{3:5}$ families from biparental crosses and intermating followed by selfing to produce $S_{1:3}$ families from 4-way crosses.

directions. Each plot occupied a 0.09-m^2 area. Experiments were surrounded by two rows of border hills of the crown rust susceptible cultivar, Markton. Soil type at this location was a Nicollet loam (fine-loamy, mixed, mesic Aquic Hapludoll).

Three tillers in each plot in the inoculated treatment whole plots were inoculated with isolate 345 of *P. coronata* at the 3 to 4 leaf stage of development (Zadoks growth stage 13–14, Zadoks et al., 1974) by injecting approximately 0.2 mL of a urediniospore suspension into each stem. Plants in the border hills were also inoculated. The fungicide treatment plots were not inoculated, but were sprayed with the systemic fungicide triadimefon to prevent crown rust disease. One fungicide application (500 g a.i. in 815 L of H_2O ha^{-1}) was made at the 4 to 5 leaf stage (Zadoks growth stage 14–15, Zadoks et al., 1974) with a motorized backpack sprayer.

Percent of leaf area infected was scored visually by a modified Cobb's scale for cereal rust (Peterson et al., 1948) on the flag leaf and second leaf of four tillers in every plot in the inoculated treatment. Disease severity ratings were made on four dates, at 3- to 4-d intervals, after symptoms appeared on flag leaves. Mean percent leaf area infected, averaged over both flag and second leaves, was computed for each plot on each rating date. AUDPC was then computed for each plot, by means of the formula of Bjarko and Line (1988). AUDPC was measured on the inoculated plots only. A second fungicide application was made 30 d after the first. The fungicide-treated plots were monitored to time reapplication of the fungicide when crown rust began to appear.

Heading date (date after planting on which the first nodes on half of the plants in the plot had emerged completely above the flag leaf) and plant height at maturity (excluding awns) were measured on each plot. All plants in a plot were bundled together at harvest and dried at ambient temperature for at least 1 wk, after which the plants were threshed and grain yield was measured on each plot. One hundred-seed weight was measured on each plot by averaging the weights of two samples of 100 seeds. After weighing seeds, the grain from each of the three plots of an entry-whole-plot treatment combination was bulked together to provide sufficient seed for measuring test weight.

F_3 seeds harvested from the F_2 bulk entries in the 1997 experiment were used to replicate the experiment in three locations in 1998: the Agronomy and Agricultural Research Farm; the Hinds Research Farm, north of Ames, Story Co., IA; and the Iowa State University Northern Research Farm, near Kanawha, Hancock Co., IA. The experimental design and execution were the same as in 1997, but three replicates were used at each location. Soil types were Coland clay (fine-

loamy, mixed, mesic Cumulic Endoaquoll) at Hinds Farm and Canisteo (fine-loamy, mixed, mesic Typic Endoaquoll) at Kanawha.

Statistical Analysis of Design II Experiment

Analysis was performed by SAS Proc Mixed (SAS Institute Inc., 1997), considering whole plot treatments and entries to be fixed effects, and environments, complete blocks, and incomplete blocks to be random effects. This overall analysis was used to estimate the main effects of whole plot treatments and entries, and the entry-treatment combination means. Main effects and interactions between entries and treatments were tested for significance in this analysis. The Design II mating analysis was conducted on the 100 F_2 and F_3 progeny entries only. To take advantage of the complete and incomplete block information provided by the parents and check entries, within-environment split-plot analyses were conducted, and means adjusted for block effects were obtained for each entry-treatment combination. The adjusted means of the progeny entries from each environment (excluding progenies of Jim) were then analyzed as a Design II by means of Proc Mixed, considering resistance donor parents, yield donor parents, and their interactions to be fixed effects, and considering environments, and interactions of environments with other factors to be random effects. Phenotypes measured in different treatments were considered to be different traits. For example, grain yield measured in inoculated plots was considered to be a separate trait from grain yield measured in fungicide-treated plots. Tolerance ratios were computed for grain yield, 100-seed weight, and test weight as the ratio of the trait mean estimated in inoculated plots to the trait mean estimated in fungicide-treated plots. Correlations among traits were estimated on the basis of progeny entry means over environments.

Random-Mated Population Evaluation

In 1998, 198 $S_{1:3}$ families representing a random-mated population were evaluated along with the parents, the susceptible check cultivar, Markton, and the crown rust resistant check cultivar, Gem. The 220 entries were arranged as an alpha lattice with 11 entries within each of 20 incomplete blocks within each of three complete replications within each treatment at each location. The experimental designs, execution, and locations were otherwise identical to the Design II experiment in 1998.

Statistical Analysis of Random-Mated Population Evaluation

The experiment consisted of both "fixed" effect entries (parents and checks), and "random" entries ($S_{1:3}$ families representing the random-mated population). Therefore, a first analysis was performed using SAS Proc Mixed in which entries and treatments were considered fixed effects, and locations, complete blocks, and incomplete blocks were considered random effects. This analysis was used to estimate the main effects of whole plot treatments and entries, the entry-treatment combination means, and the standard errors for mean comparisons. The means of each $S_{1:3}$ family for each trait-treatment combination adjusted for block effects were obtained for each location. These means (excluding those of the 36 lines descended from Jim) were then analyzed using Proc Mixed, considering families and environments to be random effects. Heritabilities were estimated on an entry-mean basis from these data, and on a plot basis from the original plot data, but excluding the parents, checks, and lines descended from Jim. Approximate standard errors of the heritability estimates were computed by the delta method (Lynch and Walsh, 1997). Genotypic and phenotypic correlations among traits were estimated by the multivariate analysis of variance option in SAS Proc GLM (SAS Institute Inc., 1990). Standard errors of the correlations were estimated following Mode and Robinson (1959).

RESULTS

Design II Experiment

Entries differed significantly for all traits measured, and entry × treatment interaction was significant ($P < 0.0001$) for 100-seed weight and test weight, but not for grain yield ($P = 0.23$). The Design II analysis indicated that rust resistance donor parents varied significantly for general combining ability for all traits tested—AUDPC ($P = 0.01$), grain yield ($P = 0.01$), 100-seed weight ($P = 0.02$), and test weight ($P = 0.006$) in inoculated plots; and grain yield ($P < 0.001$), 100-seed weight ($P < 0.001$), and test weight ($P < 0.0001$) in fungicide-treated plots. Yield donor-parent general combining ability was also a significant ($P < 0.002$) source of variation for all traits except for grain yield in fungicide-treated plots ($P = 0.06$). The significant general combining ability variation in the progeny indicates that additive genetic effects are significant for all traits in this population. Yield parent × rust resistance parent interaction was a highly significant ($P < 0.01$) source of variation for all traits, indicating that nonadditive specific combining ability effects were important for these traits in this population.

The yield donor-parent lines per se had higher mean grain yield than the rust resistance parents under both inoculated and rust-free conditions (Table 1). The rust resistance parents had better mean resistance to crown rust disease (lower AUDPC) and higher mean test weight under crown rust inoculation than the yield donor parents (Table 1). Several of the yield donor parents, such as Brawn and Hazel, however, had crown rust resistance equivalent to the most resistant resistance donor parents.

Entry mean values for grain yield, 100-seed weight, and test weight under crown rust inoculation were correlated either positively or not significantly with the same traits measured in fungicide-treated plots (Table 2). AUDPC was correlated negatively ($r = -0.42$ to $r = -0.63$) with these traits measured under crown rust inoculation, indicating that higher levels of resistance (measured as lower AUDPC scores) tended to be associated with higher grain yield and grain quality traits under inoculation. Of the traits measured in fungicide-treated plots, however, only mean 100-seed weight was negatively correlated ($r = -0.35$) with mean AUDPC. Test weight in the fungicide-treated plots was positively correlated ($r = 0.30$) with AUDPC, indicating that entries with higher levels of resistance (lower AUDPC) tended to have lower test weight in fungicide-treated plots. Grain yield and 100-seed weight in the fungicide-treated plots were positively correlated with mean heading date ($r = 0.34$ and $r = 0.37$), but mean heading date did not have a significant relationship with AUDPC or grain yield and quality traits under inoculation (Table 2).

Table 2. Correlations among 100 F_2 and F_3 oat progeny means from crosses between yield donor and rust resistance donor parent lines for traits measured under crown rust inoculation and in plots treated with a systemic fungicide to limit crown rust infection and for tolerance ratios, estimated from design II mating experiment in four Iowa environments in 1997 and 1998.

	Traits measured in crown rust-inoculated plots			Traits measured in fungicide-treated plots			Tolerance ratios			Means over rust treatments	
	100 Seed weight	Test weight	AUDPC	Grain yield	100 Seed weight	Test weight	Grain yield	100 Seed weight	Test weight	Heading date	Height
Traits measured in crown rust-inoculated plots											
Grain yield	0.61	0.34	−0.58	0.61	0.56	NS	0.52	0.20	0.28	NS	NS
100-seed weight		0.39	−0.63	0.26	0.63	NS	0.42	0.62	0.53	NS	NS
Test weight			−0.42	NS	NS	0.40	0.38	0.29	0.71	NS	NS
AUDPC				NS	−0.35	0.30	−0.47	−0.45	−0.65	NS	NS
Traits measured in fungicide-treated plots											
Grain yield					0.54	0.25	−0.34	−0.23	NS	0.37	NS
100-seed weight						NS	NS	−0.23	NS	0.34	NS
Test weight							NS	−0.30	−0.37	NS	NS
Tolerance ratios											
Grain yield								0.47	0.51	−0.27	−0.21
100-seed weight									0.52	−0.43	NS
Test weight										NS	NS
Means over rust treatments											
Heading date											0.19

† NS, not significant at $P = 0.05$. All other correlations were significant at $P \leq 0.05$.

Random-Mated Population Experiment

The main effect of crown rust inoculation on the $S_{1:3}$ families of the random-mated population and the parental and check line entries was to reduce grain yield 40% ($P < 0.07$), 100-seed weight 17% ($P < 0.05$), and test weight 21% ($P < 0.05$). Entry main effects and entry × treatment interaction effects were highly significant ($P < 0.0001$) for all three traits, indicating that entries differed both for mean grain yield, seed weight, and test weight and also for responses of these grain phenotypes to crown rust infection. The significant entry × treatment interaction observed in the random-mated population contrasts with the result of the Design II experiment, but the interactions observed in the random-mated population are applicable to predictions of selection response because this is the Hardy-Weinberg equilibrium population to which selection will be applied. The entry × treatment interactions suggest that the grain phenotypes measured under different inoculation treatments can be considered separate variables that are affected in part by unique sets of genes. Entries also differed highly significantly ($P < 0.0001$) for AUDPC for crown rust. Several families were identified that possessed favorable combinations of crown rust resistance and grain yield and grain quality (Table 3; Fig. 2).

Heritabilities on an entry-mean basis were high for all traits, ranging from 0.62 for grain yield under crown rust infection to 0.89 for AUDPC (Table 4). Heritabilities on a plot basis tended to be much lower (Table 4). AUDPC was genotypically and phenotypically negatively correlated with grain yield, 100-seed weight, and test weight under crown rust inoculation (Table 5). Lower values of AUDPC indicate higher levels of resistance to crown rust, therefore higher levels of crown rust resistance likely contributed to increased grain yield and grain weight when plots were inoculated with crown rust. On the other hand, AUDPC was not significantly correlated with grain yield and 100-seed weight and was correlated unfavorably (both genotypically and phenotypically) with test weight in fungicide-treated plots. These results are generally congruent with those from the Design II experiment. Grain yield measured under crown rust inoculation was positively genetically correlated with grain quality traits under the same conditions, and with grain yield and quality traits in fungicide-treated plots (Table 5). Seed weight measured under inoculation was positively genetically correlated with seed weight but not grain yield or test weight measured in fungicide-treated plots (Table 5). Therefore, grain yield measured under crown rust inoculation exhibited favorable genotypic correlations with all of the other traits measured.

DISCUSSION

Evaluating Partial Resistance to Crown Rust

Race-specific resistance genes may have affected our estimates of crown rust resistance in this experiment; therefore, we cannot be certain that our ratings reflected only partial resistance. Evidence for this is that the cultivar Jim was rated as only partially resistant in the field when inoculated with isolate 345, whereas Jim was completely resistant to isolate 345 as a seedling in greenhouse inoculations. Natural inoculum is prevalent in Iowa and is impossible to exclude from field trials; therefore, it is likely that races with virulence genes different than isolate 345 were a part of the inoculum population. Nevertheless, we suggest that isolate 345 dominated the inoculum population because it was artificially inoculated before natural infection was observed in this experiment or in surrounding oat plots. When it is not certain that the effects of race-specific major-effect resistances have been excluded from partial resistance measurements, Parlievliet (1992) suggested that selection be practiced against both the most resistant and least-resistant genotypes.

Timing of the ratings is critical to accurately measuring AUDPC. Crown rust severity increased quickly on the most susceptible genotypes; ratings on the same genotype taken only 3 d apart differed greatly in some

Table 3. Means of selected $S_{1:3}$ oat lines and parental and check lines for crown rust AUDPC and agronomic traits measured under crown rust inoculation and in plots treated with a systemic fungicide to limit crown rust infection, estimated from three Iowa environments in 1998.

	Traits measured in crown rust-inoculated plots				Traits measured in fungicide-treated plots			Means over rust treatments	
Line	AUDPC	Grain yield	100 Seed weight	Test weight	Grain yield	100 Seed weight	Test weight	Heading date	Height
		g m^{-2}	g	kg m^{-3}	m^{-2}	g	kg m^{-3}	dap†	m
Experimental lines									
IA97009-2	5	171	2.73	322	192	2.90	311	55	1.07
IA97027-1	79	144	2.78	317	241	3.34	372	53	0.90
IA97038-2	25	150	2.86	312	173	3.50	353	52	0.91
IA97045-1	14	128	3.08	309	184	3.13	356	52	0.81
IA97062-2	40	180	2.82	366	236	3.31	387	54	0.95
IA97066-2	67	163	2.62	318	272	3.21	348	54	1.03
IA96498-2	67	177	2.59	305	240	3.08	403	56	0.94
IA96508-1	75	150	2.72	287	287	3.07	371	57	0.96
Parental lines									
Brawn	27	175	2.64	286	291	3.26	463	60	0.97
Don	28	146	2.34	351	223	2.86	400	54	0.91
Hazel	15	143	2.32	298	271	2.69	353	62	1.03
Ogle	159	155	2.46	292	282	3.12	375	55	0.96
Prairie	47	215	2.33	299	254	3.09	379	57	0.93
Premier	277	104	2.03	258	209	2.78	396	54	0.87
MN841810	31	137	2.49	301	158	2.83	330	57	0.98
Portage	42	143	2.47	325	258	2.88	383	56	1.06
Check lines									
Markton (susceptible)‡	288	16	1.53	–	164	2.54	324	58	1.01
Gem (resistant)	12	172	3.05	324	214	3.37	360	56	0.98
LSD 0.05	71	65	0.33	57	65	0.29	57	1	0.10

† Days after planting.
‡ Markton did not produce sufficient grain under crown rust infection to estimate test weight.

cases (Fig. 2). We observed that highly infected leaves tended to senesce more rapidly than uninfected leaves. This caused some bias in our estimation of AUDPC, because we were unable to rate the highly infected, senesced leaves on the later rating dates, and therefore we tended to rate the less infected plants of the most susceptible genotypes at later dates. This effect is illustrated by the disease progress curve exhibited by the

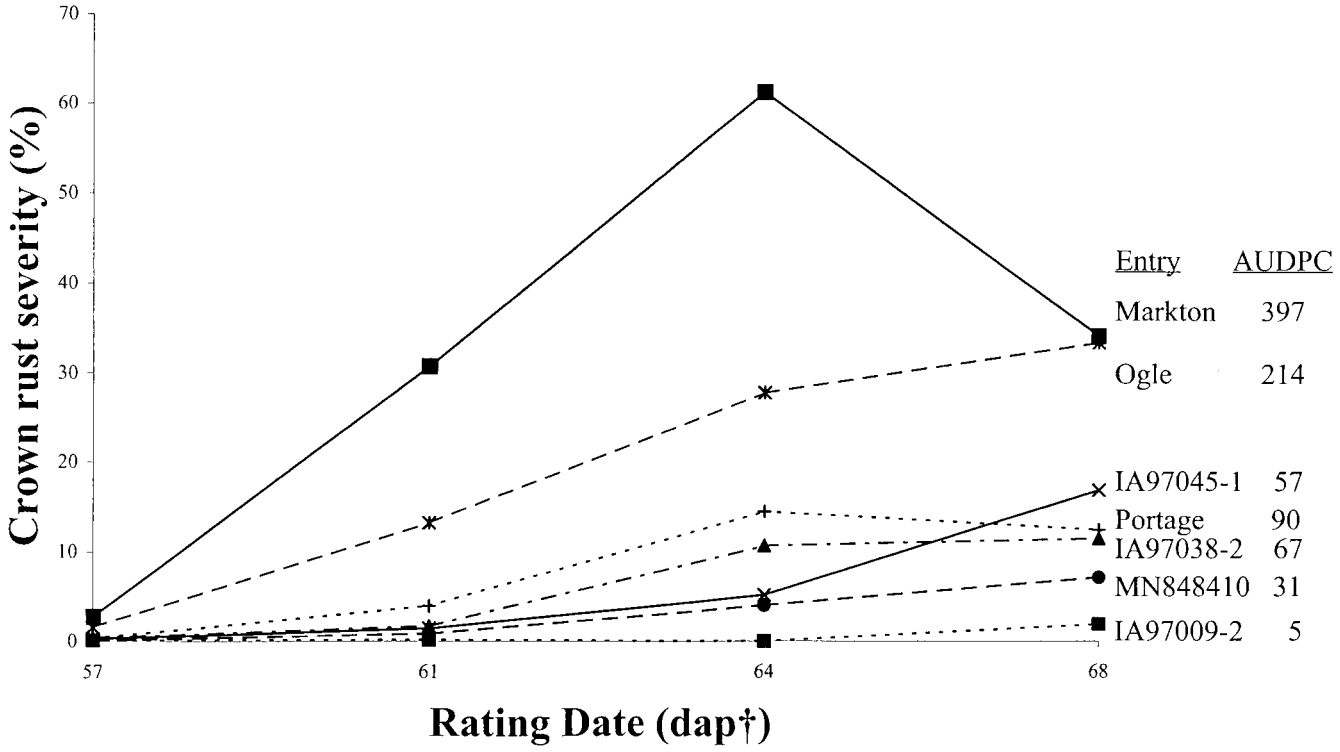

Fig. 2. Mean crown rust severity ratings of selected experimental oat lines and cultivars at each of four rating dates in Boone County, IA in 1998. Within each date, mean disease severity was estimated by measuring disease severity on four flag leaves and four second leaves within each of three replicate plots. † Days after planting.

Table 4. Heritability estimates (and their standard errors) of oat grain yield, 100-seed weight, test weight, and AUDPC measured in crown rust-inoculated plots; and grain yield, 100-seed weight, and test weight measured in plots treated with a systemic fungicide to limit crown rust infection. Estimates were based on 162 random $S_{1:3}$ oat families evaluated in three Iowa environments in 1998.

	Traits measured in crown rust-inoculated plots				Traits measured in fungicide-treated plots		
	Grain yield	100-seed weight	Test weight	AUDPC	Grain yield	100-seed weight	Test weight
Heritability on a plot-basis	0.22 (0.04)	0.58 (0.03)	0.56 (0.06)†	0.57 (0.04)	0.26 (0.04)	0.40 (0.04)	0.46 (0.06)†
Heritability on an entry mean-basis	0.62 (0.06)	0.89 (0.02)	0.80 (0.04)	0.89 (0.02)	0.72 (0.04)	0.81 (0.03)	0.72 (0.05)

† Test weight was measured on samples of grain bulked over replicate plots at a location, therefore this is heritability on a sample-basis.

susceptible check Markton, which had a mean severity of 61% on the third rating date in the random-mated population experiment at the Boone County location in 1998, but only 34% on the fourth rating date in the same environment (Fig. 2). This phenomenon tended to bias our estimates of AUDPC of the more susceptible cultivars downward.

In opposition to the effect of senescence, interplot interference probably resulted in higher AUDPC values for the more resistant genotypes than would occur in larger field plots (Patanothai et al., 1975). The inoculated border rows were intended to provide a uniformly high level of inoculum for secondary infection. We desired to make selections under conditions of high disease severity.

Despite these difficulties, AUDPC was a good measure of the rate of crown rust development on different genotypes, as shown by our ability to detect statistically significant differences among genotypes for AUDPC. The *F*-statistics for genotype effects were higher for AUDPC than for disease severity taken at any single date within locations in the random-mated population evaluation, and AUDPC integrates information from multiple dates into a single variable. Therefore, AUDPC provided the most appropriate measurement of resistance to crown rust in this population.

Parent Selection

The rust resistance parents, on average, had better resistance to crown rust disease than the yield parents, but there were several rust resistance donor parents that exhibited relatively poor crown rust resistance. The Australian parent lines, for example, had mean AUDPC values not significantly lower than the well-adapted but crown rust-susceptible cultivar, Ogle (Table 1). H632-518, which was released as a crown rust tolerant germplasm line (Simons et al., 1987), exhibited relatively good tolerance to crown rust infection in terms of test weight, but was quite low-yielding, and did not have outstanding crown rust resistance (Table 1). The poor adaptation of these lines to Iowa combined with only mediocre resistance to crown rust suggests that they did not contribute useful germplasm to the population.

Gene Action and Heritability

The progeny from the Design II mating were tested in the F_2 generation in one environment and in the F_3 generation in three environments, making precise interpretation of the rust parent × yield parent interaction (specific combining ability, SCA) difficult. The progenies tested were not highly inbred, therefore dominance gene effects may have contributed to SCA. It is likely that epistatic effects contributed substantially to the SCA variation for AUDPC and grain yield and 100-seed weight under both disease treatments, because for these traits, the yield parent × rust resistance parent interaction was highly significant even when the F_2 generation data were excluded. Stuthman and Stucker (1975) reported significant SCA variation for grain yield in highly inbred oat progeny lines, which must have been the result of epistatic effects, rather than dominance effects.

The high entry-mean heritabilities for all traits measured (Table 4) suggest that all traits should respond well to selection on the basis of line means. Heritabilities on a plot basis for grain yield, particularly, were much

Table 5. Genotypic and phenotypic correlation estimates (and their standard errors) among grain yield, 100-seed weight, test weight, and AUDPC measured in crown rust-inoculated plots; and grain yield, 100-seed weight, and test weight measured in plots treated with a systemic fungicide to limit crown rust infection. Estimates were based on 162 random $S_{1:3}$ oat families evaluated in three Iowa environments in 1998. Genotypic correlations are given in the upper right half of the table, phenotypic correlations are given in the lower left.

	Traits measured in crown rust-inoculated plots				Traits measured in fungicide-treated plots		
	Grain yield	100-seed weight	Test weight	AUDPC	Grain yield	100-seed weight	Test weight
Traits measured in crown rust-inoculated plots							
Grain yield	–	0.51 (0.09)	0.58 (0.10)	−0.63 (0.09)	0.49 (0.11)	0.24 (0.12)	0.27 (0.13)
100-seed weight	0.45 (0.07)	–	0.38 (0.09)	−0.40 (0.08)	−0.10 (0.10)	0.76 (0.05)	−0.10 (0.10)
Test weight	0.47 (0.08)	0.34 (0.09)	–	−0.44 (0.09)	0.04 (0.12)	0.07 (0.11)	0.41 (0.12)
AUDPC	−0.47 (0.07)	−0.37 (0.07)	−0.33 (0.10)	–	0.08 (0.10)	0.07 (0.10)	0.31 (0.10)
Traits measured in fungicide-treated plots							
Grain yield	0.35 (0.08)	−0.08 (0.08)	0.06 (0.11)	0.07 (0.08)	–	0.27 (0.10)	0.54 (0.09)
100-seed weight	0.21 (0.08)	0.66 (0.05)	0.09 (0.11)	0.05 (0.08)	0.25 (0.08)	–	0.17 (0.11)
Test weight	0.20 (0.09)	−0.08 (0.09)	0.29 (0.10)	0.24 (0.08)	0.46 (0.07)	0.20 (0.08)	–

lower (0.22 and 0.26, Table 4), indicating the importance of replication and multiple-environment testing for evaluating grain yield. The relatively high heritability for AUDPC, both on a plot basis (0.57) and on an entry-mean basis (0.89) suggests that evaluation of percentage of leaf area infected on two leaves on each of four plants per plot within each of several rating dates was an effective method to distinguish the partial crown rust resistance of oat lines. This result contrasts with the conclusion of Simons (1972) that heritability of partial resistance tends to be low. The genotypic variance that constitutes the numerator of these heritability estimates is an estimate of $(3/2)\sigma^2_A + (1/32)\sigma^2_D + (11/4)D_1 + (41/64)D^*_2 + (1/64)H^* + (9/4)\sigma^2_{AA}$, where terms are defined in Nyquist (1991). Given the evidence for epistatic gene effects in this population from the Design II experiment, the estimates of heritability are likely biased upward by additive × additive epistatic variance, and perhaps by other nonadditive components of genetic variance. In addition, genotype × year interaction variances are confounded with the genotypic variance component estimates since the lines were evaluated only in one year. Therefore, predictions of response to selection based on the heritability estimates presented in Table 4 are probably overestimates of the true response to selection.

Trait Correlations

The absence of strong unfavorable correlations among most traits indicated that simultaneous improvement of grain yield, test weight, and seed weight should not be unduly difficult in this population. The correlations between mean tolerance ratios and grain yield and grain quality measures illustrate the typical pattern described by Rosielle and Hamblin (1981). Under stress (in this case, crown rust infection), grain yield, seed weight, and test weight were correlated positively with tolerances for those traits (Table 2). With negligible crown rust stress in the fungicide-treated plots, grain yield, seed weight, and test weight were negatively or not significantly associated with tolerance (Table 2). Thus, selection for increased tolerance to crown rust resistance would likely result in selection for genotypes that perform better under infection, but worse in the absence of disease. Crown rust disease is endemic in the U.S. North Central region, but varies in intensity among years and among sites within states. Therefore, oat cultivars that perform well under varying levels of crown rust disease are desired. Selection for crown rust disease tolerance would likely not contribute to this goal.

Selection for increased levels of crown rust resistance (lower AUDPC) rather than tolerance in this population would be expected to result in improved grain yield, seed weight, and test weight under infection, but would not improve grain yield or 100-seed weight in disease-free conditions, and would result in lower test weight in disease-free conditions. Carson and Wicks (1989) suggested that selection for yield under disease stress will generally result in improvements in yield in both disease-stressed and disease-free environments and in disease resistance. We would make the same prediction for this population, because the observed pattern of genetic correlations suggests that selection for grain yield under disease stress alone will result in correlated improvements in the other traits of interest.

Grain yield under disease stress and grain yield in the absence of substantial disease stress can be considered distinct traits that may be under the control of different sets of genes. Population improvement for multiple traits can be achieved by different methods, including independent culling, tandem selection, or index selection (Young, 1961) If relative economic values for improvement are known, then optimal selection indices will be superior to all other methods of multiple trait improvement (Falconer and Mackay, 1996; Young, 1961). To estimate relative weights for an optimal selection index, genotypic and phenotypic variances and covariances among the traits included in the index must be known or estimated (Baker, 1986). Evaluation of random $S_{1:3}$ lines from the random-mated population permitted estimation of the relevant genotypic and phenotypic variances and covariances. Optimal index selection has not been widely used in plant breeding because relative economic values associated with different traits are generally unknown, and genetic and phenotypic covariances between traits are not routinely estimated. Carson and Wicks (1989) suggested that selection for yield under disease stress would be a good alternative to index selection for yield under stress and nonstress environments and for disease resistance because it would avoid these problems, and it would have the additional advantage of eliminating the time and expense required to make multiple disease severity ratings.

Given that we have already measured AUDPC for the lines in this population and estimated the genotypic and phenotypic covariances, however, development and use of a selection index is most appropriate. In lieu of assigning relative economic values to each of the traits, one could create an aggregate breeding value that weights standardized improvements in grain yield, seed weight, and AUDPC measured under crown rust inoculation, and grain yield and seed weight measured in fungicide-treated plots equally. A difficulty with selection for crown rust resistance will be to avoid selecting genotypes with race-specific major-effect resistance genes. While we attempted to minimize the effects of these genes, they may still have affected our results. Since the index incorporates four other traits in addition to AUDPC, selection pressure for crown rust resistance would be reduced and therefore the likelihood of selecting only major-effect resistance genes would be lessened. Advanced generation lines developed from the population could be tested later to determine if they contain race-specificic resistance genes. Another possibility is to eliminate those lines with the highest levels of crown rust resistance before developing the selection index.

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